

*DYNAMICS OF TIME DISCRIMINATION:
II. THE EFFECTS OF MULTIPLE IMPULSES*

JENNIFER J. HIGA

DUKE UNIVERSITY

According to a diffusion generalization model, time discrimination is determined by the frequency and recency of preceding intervals of time. A procedure for studying rapid timing was used to investigate whether pigeons' wait-time responses were sensitive to these factors. In Experiment 1 the number (two or eight) and spacing (consecutive or far apart) of 5-s interfood intervals (called impulses) intercalated in a series of 15-s interfood intervals (nonimpulses) were studied. Experiment 2 was identical to the first but the interfood intervals were increased by a factor of three. Overall, impulses shortened wait times in the next interfood interval. However, several impulses occurring in succession extended the localized effect of an impulse: Wait times following a set of eight-close impulses were slow to recover to preimpulse levels. The results show that linear waiting is only an approximation to the dynamic process, and a process that is sensitive to events in an animal's remote past, such as the diffusion generalization model, provides a better account of rapid timing effects.

Key words: time discrimination, dynamics, diffusion generalization model, wait time, interfood interval, key peck, pigeons

The present paper is concerned with the processes by which the duration of some stimulus controls behavior. The stimulus may be the duration of a tone or light, or the time between a time marker and reinforcer. For example, food itself is an excellent time marker (e.g., Staddon, 1974) so that after chronic exposure to schedules of periodic food reinforcement, most mammals and birds learn to withhold the instrumental response for some time after each food delivery. The postreinforcement pause or wait time is typically proportional to the interfood interval (IFI; Dews, 1970; Gibbon, 1977; Richele & Lejeune, 1980; Schneider, 1969).

The process underlying temporal control has usually been studied from a psychophysical point of view (e.g., Gibbon & Allan, 1984), with an emphasis on what an animal learns about the intervals presented during training. Furthermore, standard theories about the timing process are based on molar features of the experimental procedure. For

example, consider the dominant theoretical approaches to time discrimination: scalar expectancy theory (SET; Gibbon, 1977) and the behavioral theory of timing (BeT; Killeen & Fetterman, 1988). SET's assumptions about memory for time intervals, memory sampling rate, and thresholds of time estimates are based on statistical distributions derived from molar features of the pacemaker system or reinforcement schedule (e.g., Church & Broadbent, 1991; Gibbon, 1995; Gibbon & Church, 1984; Gibbon, Church, & Meck, 1984). BeT, too, is based on molar properties of the experimental situation. According to BeT, adjunctive responses mediate time discrimination. Such responses are assumed to be associated with transitions between states produced by pulses from a Poisson pacemaker. The pacemaker speed depends on the *average* time between reinforcers in a given context and the overall amount and probability of reinforcement (e.g., Fetterman & Killeen, 1991). By focusing on molar properties of the procedures, however, the dynamics of timing have been largely overlooked, and little is known about how time discrimination occurs.

The dynamics may have been infrequently studied in the past, perhaps in part because, with few exceptions (e.g., Gibbon & Balsam, 1981), time discrimination was assumed to be slow to develop. Indeed, steady-state performance under the usual conditions required many sessions and trials of exposure to a sin-

Research support was provided by grants to Duke University from the National Science Foundation and the National Institute of Mental Health and a Duke University Arts and Sciences Research Grant. Portions of this paper were presented at the Annual Meeting of the Psychonomic Society, November 1991. I thank Nancy Innis, Peter Killeen, George King, and John Staddon for very helpful comments on earlier drafts of the paper.

Reprint requests should be sent to J. J. Higa at the Department of Psychology: Experimental, Duke University, Box 90086, Durham, North Carolina 27708-0086 (E-mail: jennifer@psych.duke.edu).

gle interval. Exposing animals to 30 or more sessions, for example, is not uncommon (e.g., Innis, 1981; Schneider, 1969). The assumption about the speed of time discrimination may have arisen from early observations of the kind reported by Skinner (1938, p. 125). Skinner reported that wait time (i.e., a reduced rate of responding at the beginning of the IFI) developed within a few days under short IFIs but took many days to develop under longer IFIs. Perhaps most research has focused on steady-state behavior obtained from chronic procedures because of the apparent slowness in the adaptation of wait time (and other measures of discrimination).

In contrast to the results of these studies, a set of experimental results from our laboratory shows that time discrimination develops rapidly under certain conditions, occurring within a few sessions of exposure. This recent discovery suggests that some part of the timing mechanism is fast-acting, and the method we used provides an opportunity for studying the dynamics of timing.

Our procedure for studying rapid adjustments in timing involves short-term exposure to response-initiated delay (RID) schedules, which are functionally equivalent to a signaled conjunctive fixed-ratio (FR) 1, fixed-time schedule (e.g., see Shull, 1970a, 1970b, for earlier studies on RID schedules). (RID schedules have been used because they provide better control over the actual IFI duration an animal experiences.) Higa, Wynne, and Staddon (1991) found that pigeons' wait times tracked RID IFIs that changed in duration, within a session, according to a sinusoidal pattern in the sense that the output pattern of wait times matched the input sequence of IFI durations. In particular, wait time in one IFI was proportional to the preceding or current IFI duration: Correlations between the input and output patterns were often highest at phase lags of one or zero. Therefore, the shortest or longest wait time occurred either during the shortest or longest programmed IFI (phase lag of zero) or in the next IFI (phase lag of one). Furthermore, there was little evidence of cyclic changes in wait times during a free-run period of each session in which all IFIs were of constant duration.

The effects described above occurred after a few sessions of exposure (sometimes by the

second or third session), and the speed with which wait times changed was surprising for at least two reasons. First, previous experiments often required 30 sessions or more for stable responding during a single interval within the range of intervals used in the sinusoidal sequence (e.g., Schneider, 1969). Second, pigeons' wait times tracked cyclically varying IFIs even when the sequence varied (in length and phase) across sessions. In addition, a cyclic pattern of wait times during cyclically changing IFIs and no periodicity in wait times during the free-run phase provided evidence of a timing mechanism that was sensitive to rapid changes in IFI duration.

The simplest possible mechanism consistent with these results is that wait time in IFI_{n+1} is determined by IFI_n ; this is called *linear waiting* (Wynne & Staddon, 1988). In a second experiment, Higa et al. (1991) demonstrated this process directly, using a single-impulse procedure and pigeons as subjects. Their method was simply to intercalate occasional short IFIs (5 s, called an impulse by analogy with linear systems analysis) into a long sequence of longer IFIs (15 s, called nonimpulse IFIs). They looked at wait times following an impulse to see whether wait times decreased, as implied by a "one-back" process. It turned out that an impulse did, indeed, decrease wait time in the immediately following IFI, and the decrement was localized, occurring in the next IFI only. Wait times in subsequent IFIs returned to levels observed in the IFIs preceding the impulse. The effect of an impulse did not change systematically across sessions. Especially surprising was the fact that the birds did not appear to learn that each session contained a single impulse and that IFIs following that impulse returned to longer durations. After all, responding early in a long interval does not cause reinforcement to occur sooner than programmed.

Despite its simplicity, linear waiting fits a considerable range of dynamic data. For example, in one experiment Wynne and Staddon (1988) tested a surprising implication of linear waiting. Pigeons were given a sequence of intervals that changed dynamically such that the duration of the current interval was a constant proportion of wait time in that interval. According to linear waiting, such a relation would cause wait time in the *next* inter-

val to increase or decrease without a limit, depending on whether the variable representing the proportion by which an interval changed was greater or less than one. Wynne and Staddon showed both effects: progressive increases or decreases in wait time as a function of changes in the proportion variable in individual animals within a single experimental session.

Although linear waiting provides a reasonable approximation to some data from rapid time discrimination on interval reinforcement schedules, it fails to predict other well-established experimental results from interval schedules of reinforcement. First, linear waiting is inconsistent with performance on variable-interval (VI) schedules with successive IFIs that vary in duration. It predicts that wait times should track this random series, but they do not: Wait time is typically essentially constant, that is, the same after every food delivery (see Ferster & Skinner, 1957, for examples).

Second, perhaps a more surprising finding is that pigeons do not appear to learn simpler and predictable sequences of IFI durations, such as a repeating sequence of 12 1-min intervals followed by four 3-min intervals (Staddon, 1967). Linear waiting predicts short wait times during the 1-min intervals, longer wait times during the 3-min intervals, and a delayed change in wait times from short to long and back down to short by one IFI (as the square-wave sequence cycled through a session). Instead, Staddon's pigeons waited approximately the same amount of time in all IFIs (30 s on average), even after many training sessions. Yet, when successive IFIs vary smoothly and cyclically, wait time tracks the changes in IFI duration in a way that is reasonably consistent with linear waiting, and tracking is immediate (Higa et al., 1991; Innis, Cooper, & Mitchell, 1993).

Third, an intermediate case of linear waiting has been reported: When the sequence of intervals was short (a cycle of four IFIs, 15, 5, 15, 45 s), pigeons initially tracked the sequence according to a linear waiting process. However, tracking eventually disappeared and was replaced by a VI-like performance; that is, a postfood wait time appropriate to the shortest IFI duration (Higa, Thaw, & Staddon, 1993).

These studies suggest that linear waiting is

probably an approximation to some more general process, one that underlies one-back time discrimination and failures to track according to a one-back process, as well as intermediate cases. What is the more general process? As far as we know, although standard models have occasionally been applied to dynamic situations such as acquisition (e.g., SET; Meck, Komeily-Zadeh, & Church, 1984) and to schedules with more than a single IFI (Mellon, Leak, Fairhurst, & Gibbon, 1995), they do not predict the single-impulse effect and intermediate cases of linear waiting.

A recently proposed model, the diffusion generalization model (DG; Staddon & Higa, 1991), provides suggestions about how the dynamics of timing might occur. According to a DG model, time discrimination is linked to an animal's memory for reinforced postfood times (i.e., IFIs). Postfood times are represented in memory like other stimulus dimensions (e.g., wavelength, size) by a discrete linear continuum of units (i), each with its own activation strength (X_i). X_i changes with time according to the following equation, written in discrete time (see Staddon & Higa, 1991; Staddon & Reid, 1990):

$$X_i(t) = \alpha X_i(t-1) + [(1-\alpha)/2] \cdot [X_{i-1}(t-1) + X_{i+1}(t-1)] + S_i(t), \quad (1)$$

where $X_i(t)$ is the activation strength of a unit (i) at real time t ; $X_{i-1}(t-1)$ and $X_{i+1}(t-1)$ represent activation strengths of two adjacent units at time $t-1$; and α is a diffusion rate parameter. $S_i(t)$ is set to either 1 or 0: If reinforcement occurs at postfood time t , then unit i corresponding to t is incremented. In other words, reinforcement at a particular postfood time increases the activation strength of the unit that represents this time. Activation strength of that unit generalizes and diffuses to other neighboring units according to the equation given above. Figure 1 illustrates the general mechanics of the model. It shows the effect of a single reinforcement at postfood time 5 s. Each panel shows the state of the model (i.e., activation strengths of units) at different times since reinforcement. Immediately after reinforcement, specifically one iteration (a time step, equivalent to a second of real time in this ex-

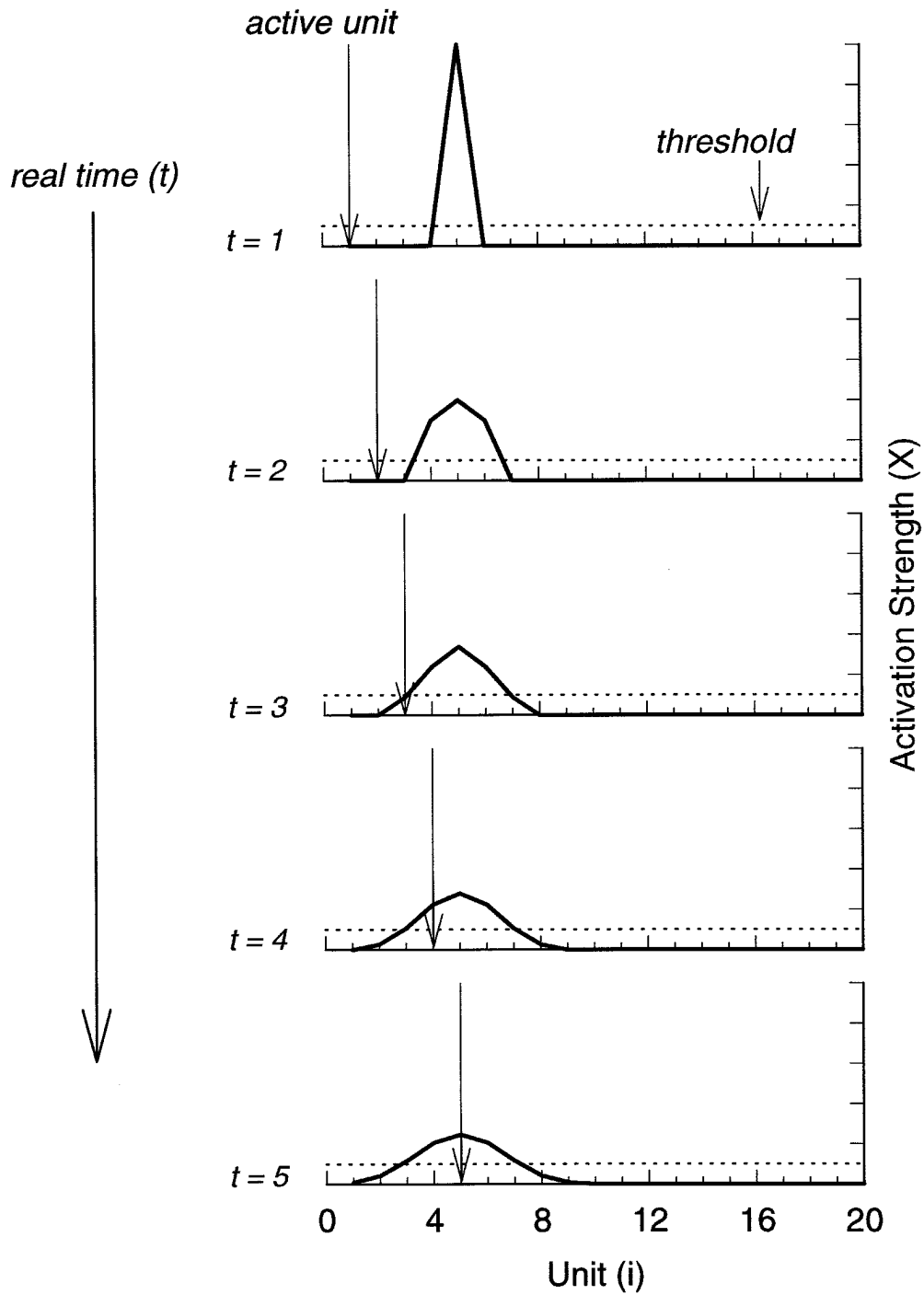


Fig. 1. Illustration of the mechanics of the DG model. Each panel shows the state of the model after different time steps following a single reinforcement at postfood time 5 ($\alpha = .4$, $\theta = .1$). The dashed horizontal line marks the threshold for responding.

ample) after reinforcement, Unit 5 increases in activation strength. In the next panel, two iterations after reinforcement, the activation strength of Unit 5 decreases, but activation has spread to surrounding Units 4 and 6. The remaining panels show how the gradient centered around Unit 5 spreads with time. If no other reinforcement occurs, the gradient will eventually flatten and the strength of all units will approach zero.

Response strength—output of the system, $V_i(t)$ —depends on a clock-like process. The units are tied to real postfood time and are potentially active one at a time: At real time t , the corresponding unit i is active if it exceeds a threshold, θ . The dashed horizontal lines in Figure 1 mark a threshold that remains constant in time. Vertical arrows mark which unit is active at each iteration. This arrow moves toward the right with each iteration or clock tick. According to this example, then, at Real Time 1, the activation strength of Unit 1 is below the threshold and is not active, so the output will be 0; at Real Time 2, Unit 2 is inactive; at Real Time 3, Unit 3 is active (this translates to a measure of wait time); at Real Time 4, Unit 4 is active, and it has a higher activation strength than Unit 3 did when it was active; finally, at Real Time 5, Unit 5 is active.

In its present form, the model predicts several effects from interval schedules (see Stadon & Higa, 1991, for details). For the present purpose, the model suggests that the dynamics of time discrimination depend on at least two factors: the *frequency* and *recency* of individual IFIs an animal experiences. First, because the activation strength (height) of the gradient increases after each reinforcer, the overall form of the gradient (and wait time) depends on the frequency of reinforcement at a particular postfood time. Second, because the process is dynamic—gradients rise and decay between each reinforcement according to α —the overall form of the gradient also depends on how long ago reinforcement at a postfood time occurred. For example, a short IFI will affect subsequent wait times in different ways, depending on whether it occurred a few IFIs ago or several sessions ago. Unlike current timing models (i.e., SET and BeT) the DG model is not based solely on the molar properties of the experimental condition: It is sensitive to

properties of individual IFIs, and can, therefore, potentially account for the rapid timing effects described earlier.

The purpose of the present experiments was to study the dependence of wait-time responses on the frequency and recency of prior IFIs. Our approach was to evaluate the model under four conditions, based on Higa et al.'s (1991) single-impulse procedure described earlier. The frequency of IFIs was tested by varying the number of consecutive shorter IFIs (impulses) intercalated in a series of longer IFIs (nonimpulse intervals); recency was studied by varying the spacing among a constant number of impulses. Figure 2 presents an example of the four different input sequences. In the two-close and eight-close conditions, the number of impulses varied but their spacing remained constant (no separation); the same held for the two-far and eight-far conditions, except that each impulse was separated by four longer (nonimpulse) intervals. In Experiment 1 the impulses were 5 s in duration and nonimpulses were 15 s. Experiment 2 was identical to Experiment 1 but the duration of impulses and nonimpulses was increased threefold. Changing the duration of the intervals allowed us to find out (within the same subject) whether the dynamics observed in Experiment 1 depended on the absolute duration of the IFIs and whether possible floor effects could account for the pattern of wait times during impulse intervals.

EXPERIMENT 1: THE EFFECTS OF THE NUMBER AND SPACING OF IMPULSES ON WAIT-TIME RESPONSES

The aim of this experiment was to test, experimentally and through simulations of the DG model, the dependence of wait times on variations in number and spacing of prior intervals. In conducting the simulations, features of the experimental conditions (see details in Procedure section) were modeled closely. Specifically, (a) an iteration (time step) was equivalent to a second of real time; (b) the parameter α was set to .18 and θ was 2.1 in all conditions; (c) 500 units were used; (d) each simulation lasted for 10 sessions per condition (100 intervals per session), and the

Place holder for corrupted page 122 of Higa et al., 1996, 66, 117-134.

It contains Figures 2 and 3 on interfood intervals, plus the words:

state of the model after each session was carried over to the next session; (e) reinforcers were presented for two iterations; and (f) the location of the first impulse (of a set of impulses) varied across simulated sessions.

Figure 3 presents the simulation results for the sequences given in Figure 2. Only a subset of simulated wait times is shown. Because the simulations showed no change in wait times during preimpulse intervals, we decid-

vgl

3November2004

ed to concentrate on changes that occurred during a set of impulses and the next 15 post-impulse intervals. Wait times during these intervals were normalized according to the mean wait time in preimpulse intervals, calculated separately for each condition. Hence, wait-time duration is shown as changes relative to preimpulse levels.

The simulations reveal several effects predicted by the DG model. First, each impulse should shorten wait time in the *next* IFI, according to linear waiting. Second, unlike linear waiting, the model predicts different patterns of wait times in intervals after each set of impulses. Specifically, recovery of wait times should be slower following eight consecutive impulses (eight-close condition) than after just two (two-close condition) in terms of the number of IFIs that elapse before wait times reach preimpulse levels. Remember that intervals following a set of impulses are of constant duration and are longer than impulses. Therefore, these non-impulse intervals provide an opportunity to observe whether wait times are affected by a set of impulses. Third, the slow recovery following eight-close impulses should be attenuated (i.e., recovery should be faster) when each impulse is separated by four longer non-impulse intervals (eight-far). According to the model, interruption of impulses by longer IFIs prevents accumulation of the tendency to respond short from each impulse, by allowing the overall activation gradient (surrounding units representing short postfood times) to dissipate. Fourth, the simulations show systematic changes in the local effect of an impulse (its effect on wait time in the next IFI): Each impulse should produce shorter and shorter wait times in all conditions except two-far. To see this, compare the level of wait time following the first and last impulse of the two-close, eight-close, and eight-far conditions. Finally, the effect of an impulse (to shorten wait time in the next IFI) should be greater when impulses occur in succession than when they are separated.

METHOD

Subjects

Four pigeons (*Columba livia*; 3 Silver Kings and 1 White Carneau) served as subjects. All had experience on various reinforcement

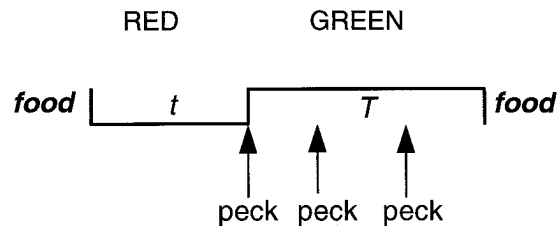


Fig. 4. Illustration of a single response-initiated delay (RID) interfood interval. t represents wait time; T represents the delay to reinforcement following the first response.

schedules, and 3 (B16, B145, and B174) had participated in other timing experiments. Each bird was maintained at approximately 80% of its free-feeding body weight. Weights sometimes increased above 80%. To limit weight gain, pigeons were sometimes studied only 6 days per week.

Apparatus

The experiment was conducted in a standard operant conditioning chamber (40 cm wide, 32 cm deep, and 34 cm high). On the front panel was a response key (1.5 cm in diameter) that could be back-illuminated either red or green. Mixed grain served as the reinforcer and was presented through an aperture (5.5 cm by 4.5 cm) placed below the key, 9.5 cm from the ceiling. A fan masked extraneous noise. A houselight, located on the chamber's door, provided illumination. The experimental events were controlled and recorded by a computer in an adjacent room.

Procedure

For all conditions a session began with delivery of a reinforcer (2-s access to mixed grain) followed by 100 IFIs. IFIs were programmed according to a RID schedule (see Figure 4). The first key peck following a reinforcer, defined as the wait time (t), was accompanied by a distinct change in the color of the response key from red to green. Subsequent key pecks were recorded but did not affect the IFI duration. The delay to reinforcement (T) following the first response was adjusted so that t and T equaled a programmed duration. After T seconds had elapsed, the green light was extinguished, reinforcement was given, and the next IFI began. The duration of T was based on the pigeon's wait time, t , and the programmed IFI

Table 1

The order of conditions for each subject in Experiment 1.

Subjects	Order of conditions	Number of sessions
B16 and B145	Baseline	10
	Two-close	10
	Baseline	10
	Two-far	10
	Baseline	10
	Eight-far	10
	Baseline	10
	Eight-close	10
B173 and B174	Baseline	10
	Two-far	10
	Baseline	10
	Two-close	10
	Baseline	10
	Eight-close	10
	Baseline	10
	Eight-far	10

duration such that $T = \text{IFI} - t$. For example, suppose that the duration of an IFI was programmed to be 15 s. If a pigeon's first peck occurred 5 s after the start of the IFI (i.e., the wait time was 5 s), then T was set to 10 s. If it waited 9 s, then T was set to 6 s, and so forth. If the pigeon waited longer than the programmed IFI duration, there was a short delay to food ($T = 0.5$ s), the green keylight was momentarily lit for 0.5 s, and food was delivered immediately.

All subjects were exposed to four experimental conditions (two-close, two-far, eight-close, and eight-far) and each condition was preceded by a baseline condition. Table 1 presents the order of conditions and the number of sessions per condition for each bird. During baseline conditions, all IFIs were programmed to be 15 s in duration. The experimental conditions differed from baseline in that some IFIs were impulses (5-s IFIs); they also differed from each other in the number and spacing of impulses (see Figure 2).

The two-close condition consisted of 98 nonimpulse IFIs and two impulses that always occurred in succession (from now on called a set of impulses). The location of a set of impulses was randomized across sessions with the following constraint: The set was always preceded and followed by at least 15 nonimpulse IFIs. This constraint implies that the first impulse of a set could occur anytime after the 15th IFI but before the 86th IFI. Con-

dition two-far was similar to two-close except that the two impulses were always separated by four nonimpulse IFIs (impulses linked by intervening nonimpulse IFIs are also called a set). The eight-close and eight-far conditions were identical to the two-close and two-far conditions, respectively, except that eight (instead of two) impulses were used.

RESULTS

Data analyses of observed wait times are based on a subset of IFIs from each session; specifically, wait times from a set of impulses and the surrounding 15 nonimpulse IFIs. Given that subjects received only 10 sets of impulses per condition (one set per session, 10 sessions per condition), wait times in these selected intervals are averaged across all sessions. The results for each subject and the group are given in Figure 5. For easier comparison with the simulation results, and because of the different overall levels of wait times across subjects, wait times for each subject (t) were normalized (t') so that $t' = t/t_{\text{mean}}$, where t_{mean} is the mean wait time in the intervals preceding a set of impulses (calculated separately for each subject).

Across conditions, wait time following most impulses decreased below preimpulse levels. However, the size of the change in response to an impulse varied across subjects. For example, birds at the extremes were B174 (large changes in wait times) and B173 (relatively small changes). As a group, impulses decreased wait time by a proportion ranging from .3 to .5.

To determine whether the effect of an impulse changed across sessions, we compared wait time in the first impulse interval against wait time in the next IFI. These data are shown in Figure 6 as cumulative records. Although each series consists of only a few data points (10 per condition) and although the effect of just the first impulse is considered, the cumulative records show two features. First, wait time was generally shorter in the interval following an impulse: Most open circles are below the filled circles as expected, if an impulse shortened wait time in the next interval. Overall, the curves for Subject B173 show the smallest effect. Second, there is little evidence of gradual learning across sessions. This is another reason the data were averaged across all sessions (see Figure 5). Wait times

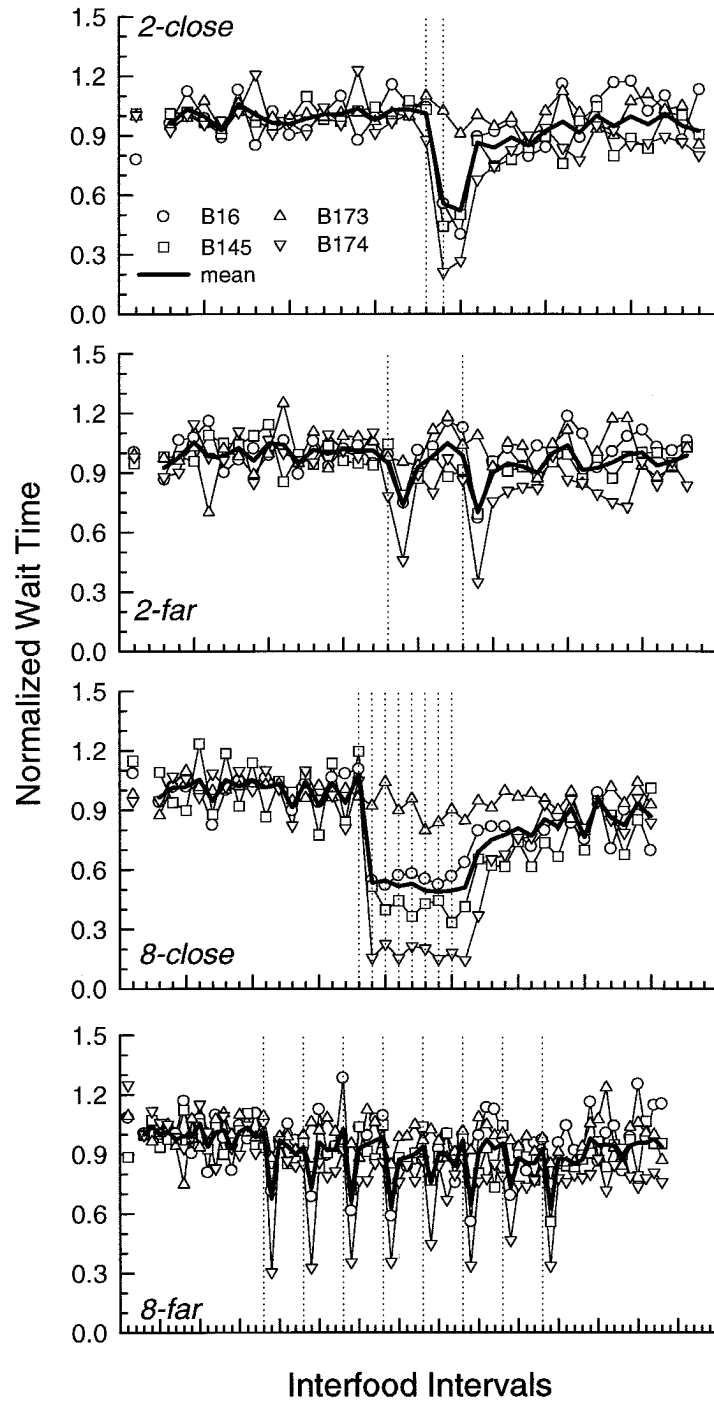


Fig. 5. Results from Experiment 1. Data are normalized mean wait times from a set of impulses and the preceding and following 15 nonimpulse IFIs. The results for each subject are shown, as is the group mean (heavy solid line). Dashed vertical lines mark the occurrence of an impulse, and open symbols near the y axis mark mean wait time during the previous baseline condition.

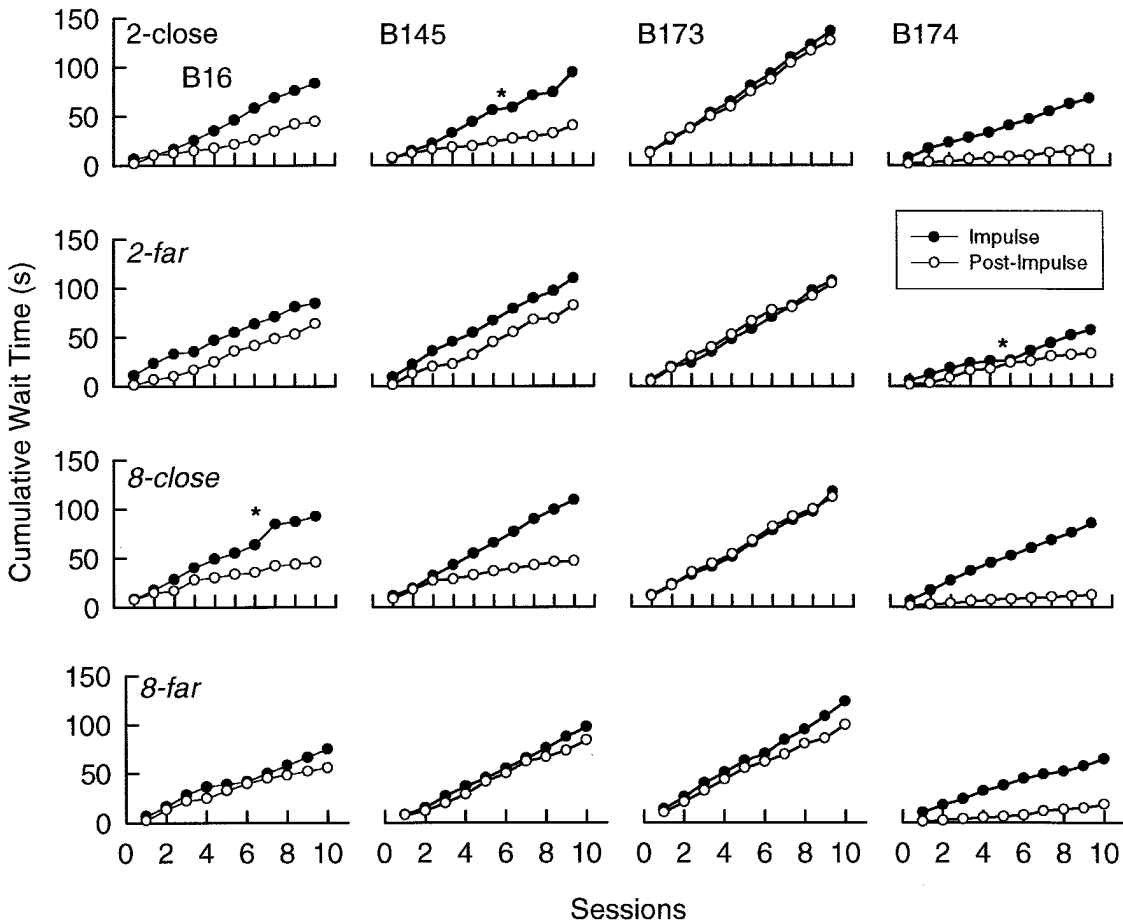


Fig. 6. Cumulative wait times for first impulse interval (filled circles) and next interval (open circles) from the different conditions of Experiment 1. Note that the slope of each series indicates how wait times changed across sessions; steeper slopes indicate cumulation of longer wait times. If the two series are identical and fall on top of each other, then there is no difference in wait time; if the two series are separated but parallel to each other then wait times start off at different values and do not change across sessions.

after the first impulse show occasional shifts across sessions, but the changes are usually abrupt (some instances are marked with asterisks in the figure), and the changes are in both directions: (a) increases in the slope, indicating a lengthening in wait time; and (b) decreases in the slope, showing that wait time was getting shorter. Perhaps the only subject to show a trend was Subject B145 during the eight-close condition.

Key results are the local effects of an impulse and their effects on wait times in postimpulse intervals. To focus on these features of responding, the relevant data from Figure 5 are replotted in Figure 7. What happened to wait times during postimpulse IFIs? In-

creasing the number of consecutive impulses from two to eight (cf. two-close and eight-close) resulted in a slower recovery of postimpulse wait times to longer durations. Increasing the number of spaced impulses (two-far, eight-far) did not produce differences as noticeable in the recovery patterns. The spacing of impulses had different effects on recovery, and depended on the number of impulses involved. Recovery after the two-close set of impulses was slightly slower than after the two-far set. On the other hand, recovery after eight-close was much slower than after eight-far impulses.

Next, what was the local effect of an impulse? The DG model predicts that wait times

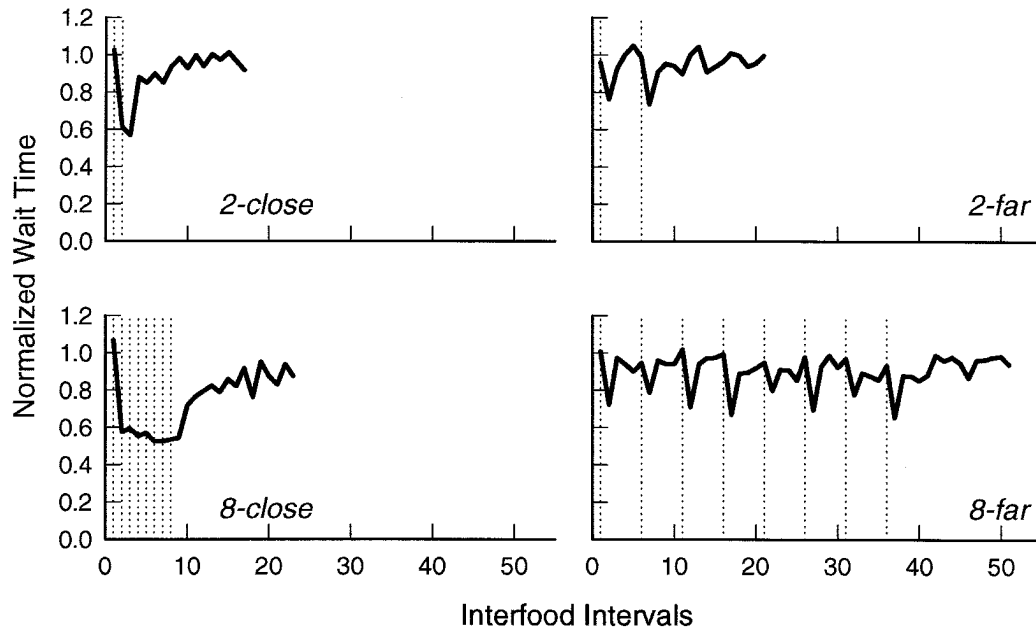


Fig. 7. Results for pigeons from Experiment 1. Only wait times (normalized, see text for details) from the set of impulses and the next 15 IFIs are shown. Data are extracted from Figure 5 for comparison with the simulation results shown in Figure 3.

following each consecutive impulse should produce consecutively shorter wait times (see Figure 3). Evidence of this effect is seen in the group means. However, individual subjects did not always show the same changes in wait times. For example, for the two-close condition in Figure 5, only 2 birds showed a decrease in wait time from one impulse to the next, and the other birds showed slight increases.

In addition, the DG model predicts an interesting effect between each impulse of the eight-far condition (Figure 3). The pattern of wait times between the first and second impulses is predicted to differ from that between the last two impulses. Between the seventh and eighth impulses, wait time should be slow to recover to levels similar to those under preimpulse IFIs. Moreover, an overall decreasing trend in wait times across the non-impulse IFIs should be evident. The individual data are too variable to discern effects between impulses, but the data in Figure 7 suggest some evidence of a slight decline in wait times across nonimpulse IFIs.

The DG model also predicts that impulses should affect wait times more (i.e., shortened wait times) when impulses occurred close to-

gether than when they were far apart. The observed grouped data show this pattern: Compare the effect of an impulse from the two-close condition with that from the two-far condition, and compare the results from the eight-close condition with those from the eight-far condition. In both sets of comparisons, wait times were generally shorter after impulses in the close than in the far conditions. Finally, the DG model predicts full recovery of wait times following a set of impulses. Such recovery was observed under all conditions except for the eight-close: Wait times did not fully recover to preimpulse levels, even by the 15th postimpulse interval, at the group and individual levels of analysis.

DISCUSSION

In this experiment we tested the DG model's predictions about how the number and spacing of impulse intervals affect time discrimination, measured as changes in wait-time duration. Overall, the results agree with several predictions of the model, the most notable of which was a decrease in wait time after each successive impulse. This result can also be explained by linear waiting, but other standard models of time discrimination do

not predict these kinds of rapid, immediate changes in wait times. Furthermore, wait times were slower to recover after a set of eight impulses when those impulses were presented close together than when they were separated (eight-far condition). This result cannot be readily explained by linear waiting or other standard models. The DG model predicts such changes based on interactions between activation gradients centered around the impulse and nonimpulse post-food times.

According to the model, the effect of a short impulse on wait times can be either localized or extended across several subsequent intervals. Increasing the number of closely spaced impulses increases the tendency to respond short because (a) the activation of an excitatory gradient centered around the time of an impulse increases, and (b) the effect spreads (diffuses and generalizes) to neighboring postfood times (see Figure 1). Therefore, the local effect of an impulse IFI, which normally changes wait time in just the next interval, may persist and affect several subsequent IFIs. Persistence of the tendency to respond short occurs when a sequence of IFIs contains many consecutive impulse intervals. Furthermore, separating each impulse by four longer nonimpulse intervals localizes the effect of an impulse (to the next adjacent IFI) because the gradient of activation around the impulse postfood time will have dissipated before the next impulse (for a given fixed set of values for α and θ).

Differences were found between the simulations and the data, however. For example, the model predicts consecutively shorter wait times following each impulse in the two-close and eight-close conditions and to some extent in the eight-far condition. Not all animals showed this effect: Wait times after each consecutive impulse sometimes remained the same or increased, slightly, in duration. Also, it is not clear why the wait times for Subject B173 did not always decrease in response to an impulse.

The particular duration of IFIs used might explain these differences. Five-second impulses produced wait times between 2 and 4 s, and a floor effect might explain why wait times did not decrease with each successive impulse. The short duration of the IFIs may also explain why impulses failed to change

wait times of Subject B173. Because wait times for this bird were usually longer than the impulse duration (13 to 15 s), it did not experience a shorter than normal IFI. Recall that in these cases (which happened infrequently except in this subject), the keylight changed from red to green for 0.5 s and food was immediately given. To study these possibilities, the next experiment tested the same birds under the same conditions as in Experiment 1, except that the durations of impulse and nonimpulse IFIs were increased by a factor of three. Experiment 2 also provided an opportunity to study how the dynamics of wait-time adjustment depend on the absolute duration of the IFIs used.

EXPERIMENT 2: THE EFFECTS OF LONGER INTERFOOD INTERVALS

Experiment 2 was a replication of the first but with longer IFIs: Nonimpulse IFIs were programmed to be 45 s and impulse IFIs were 15 s. Figure 8 presents the results of simulations for the sequences and interval durations to be tested with pigeon subjects. The simulations were conducted in the same manner as those in Experiment 1, with the same parameter values. As before, each iteration of the model was equivalent to 1 s of real time, and the data are normalized according to the same methods. Overall, the simulations show the same kinds of effects as those for 15- and 5-s IFIs.

METHOD

Subjects, Apparatus, and Procedure

The subjects and apparatus were the same as those used in Experiment 1. The procedure and conditions were identical to those of Experiment 1 except that impulse and nonimpulse IFIs were programmed to be 15 and 45 s in duration, respectively; see Table 2 for the order of conditions and number of sessions per condition.

RESULTS AND DISCUSSION

Data analyses and figures are based on the methods from Experiment 1. Figure 9 presents normalized mean wait time during a set of impulses and the 15 preceding and following IFIs. Across conditions, the wait times for

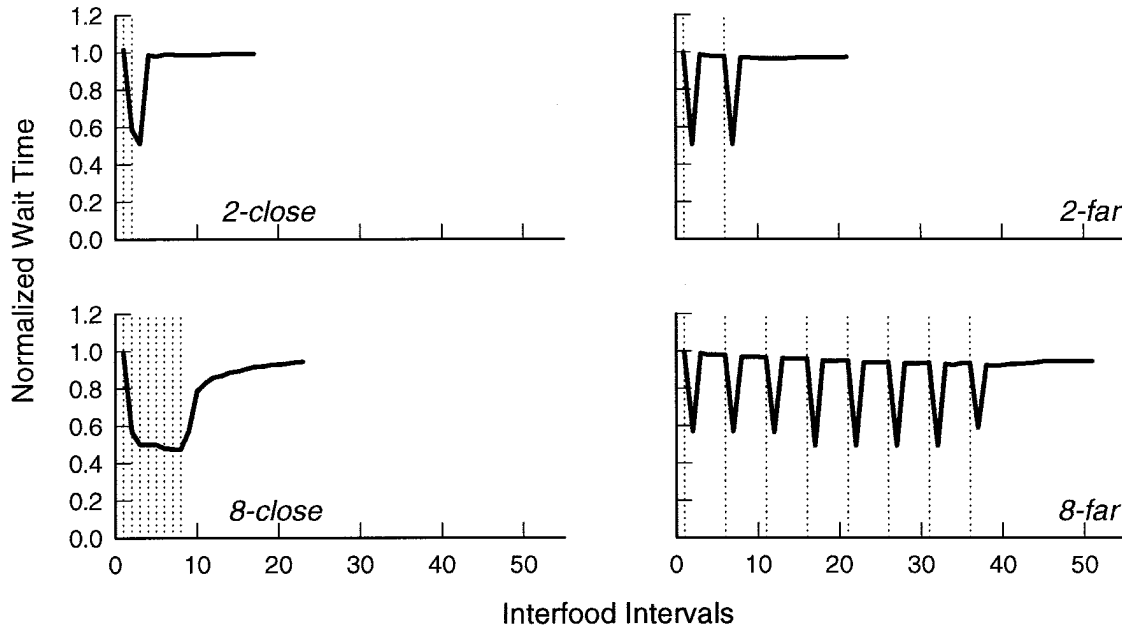


Fig. 8. Results of simulations for conditions from Experiment 2. Only wait times (normalized, see text for details) from the set of impulses and the next 15 IFIs are shown.

most birds showed a local effect of an impulse IFI: An impulse reduced wait time in the next IFI. Again, the birds appeared to track changes in IFI duration according to a linear waiting process. Even Subject B173, who showed weak impulse effects in Experiment 1, responded with consistent decreases in wait-time duration after most impulses in

each condition. Apparently, increasing the duration of impulse and nonimpulse IFIs ensured that this bird experienced a shorter than normal IFI.

The cumulative records of wait times from the first impulse IFI and the next IFI (Figure 10) show little systematic change in the effect of an impulse across sessions. Like the results from Experiment 1, wait time was generally shorter in the interval following the first impulse. That is, most open circles are below the filled circles, as would be expected if an impulse shortened wait time in the next interval. Only a few exceptions are evident (e.g., Subject B145 during the first few sessions of the two-far condition and Subject B173 in the two-far condition). In addition, little evidence of gradual learning across sessions was found. Wait times after the first impulse occasionally shifted across sessions, but the changes were usually abrupt, occurred in both directions, and occurred at different points across sessions for different birds.

Figure 11 presents the data from a subset of IFIs (during the set of impulses and post-impulse IFIs) extracted from Figure 10 so that the results can be more easily compared with the predictions of the DG model (Figure

Table 2

The order of conditions for each subject in Experiment 2.

Subjects	Order of conditions	Number of sessions
B16 and B145	Baseline	16
	Two-close	10
	Baseline	10
	Two-far	10
	Baseline	10
	Eight-far	10
	Baseline	10
	Eight-close	10
B173 and B174	Baseline	16
	Two-far	10
	Baseline	10
	Two-close	10
	Baseline	10
	Eight-close	10
	Baseline	10
	Eight-far	10

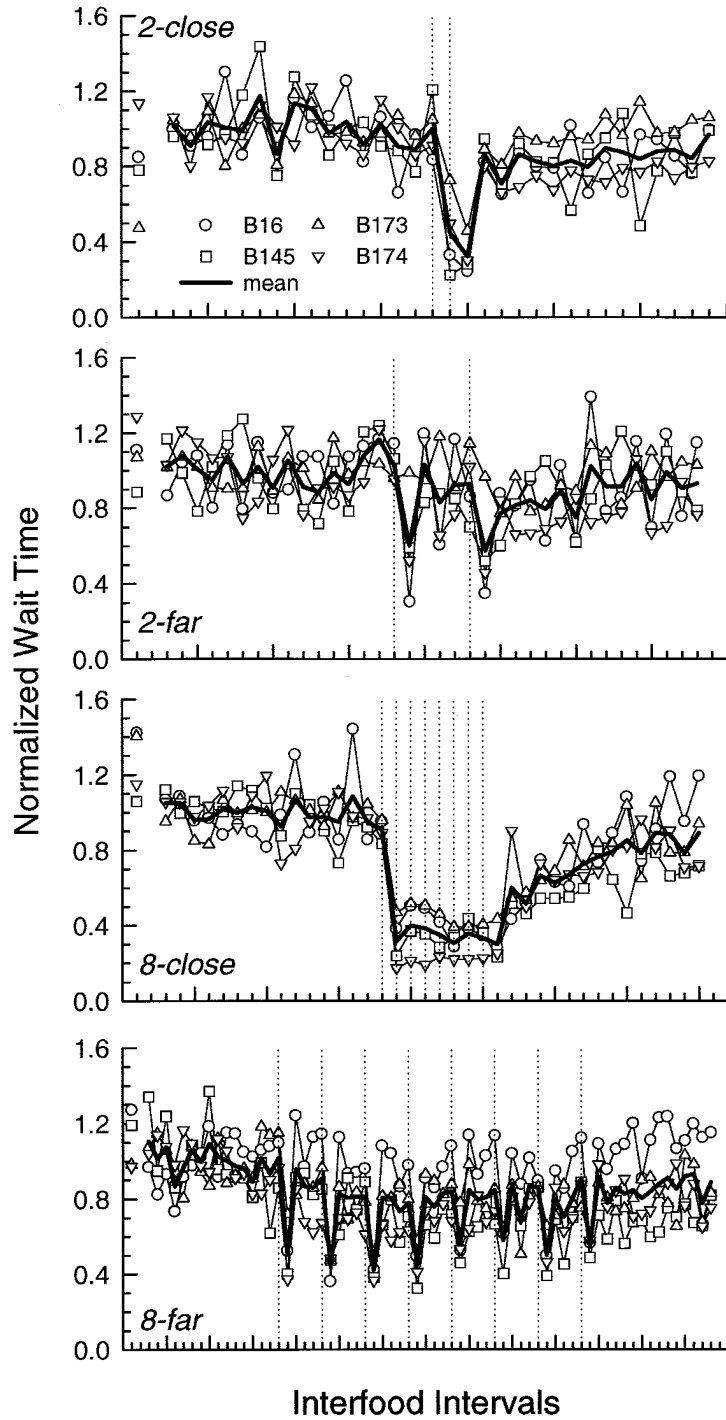


Fig. 9. Results from Experiment 2. Data are normalized mean wait time from a set of impulses and the preceding and following 15 nonimpulse IFIs. The results for each subject are shown, as is the group mean (heavy solid line). Dashed vertical lines mark the occurrence of an impulse, and symbols near the y axis mark mean wait time during the previous baseline condition.

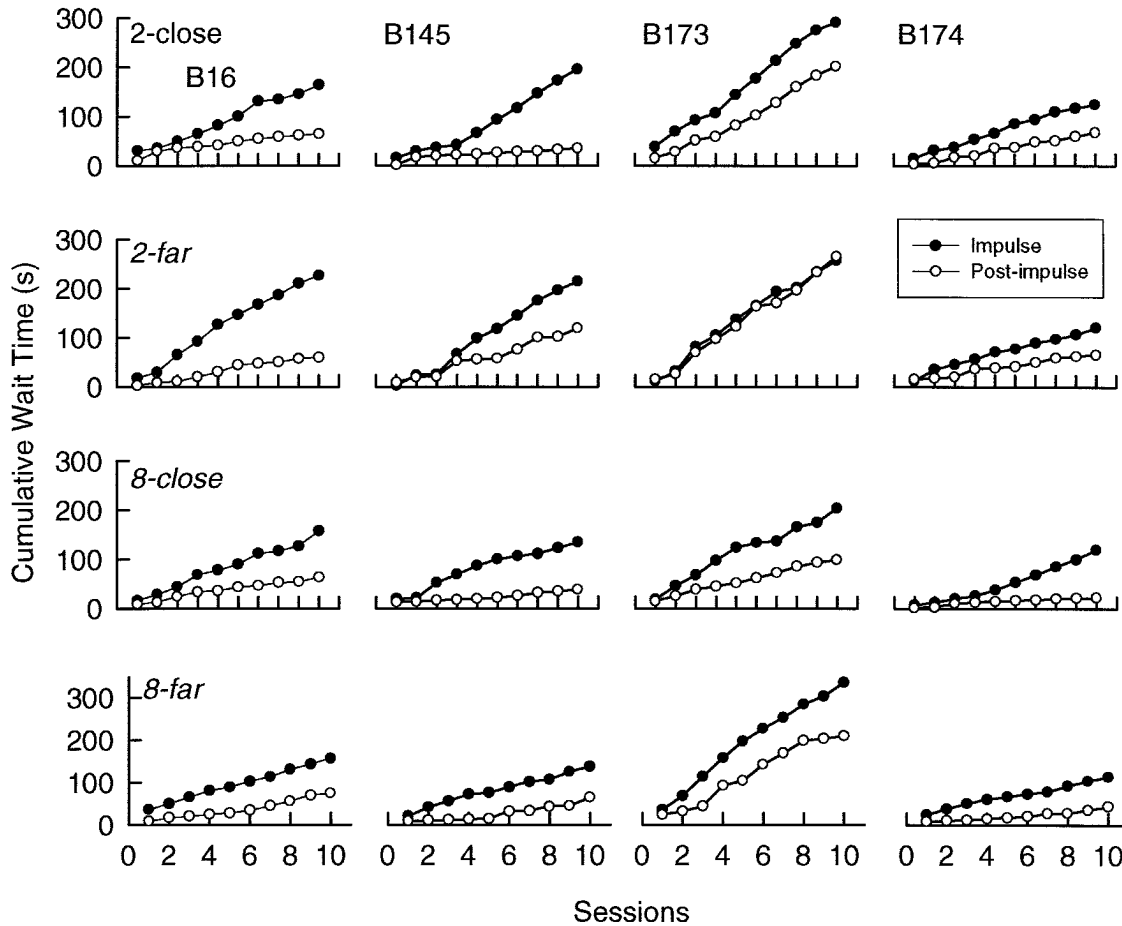


Fig. 10. Cumulative wait times for first impulse interval (filled circles) and next interval (open circles) from the different conditions of Experiment 2. Note that the slope of each series indicates how wait times changed across sessions; steeper slopes indicate cumulation of longer wait times. Also note range represented in y-axis scale.

8). The obtained results show a close correspondence to the predictions of the DG model. Two differences are worth noting. First, the rate of change in wait times across successive postimpulse IFIs under the eight-close condition was slower than predicted. Second, in the two-far condition, wait times across postimpulse IFIs appeared to recover gradually instead of quickly as predicted by the DG model. Finally, for some subjects, wait time appeared to be shorter following impulses in the two-close and eight-close conditions than in the two-far and eight-far conditions. Closer examination of the data from individual subjects, however, indicates that not all subjects showed changes in the same direction.

GENERAL DISCUSSION

Experiments 1 and 2 revealed several dynamic properties of pigeons' responses to rapid changes in the temporal sequence of IFIs that are consistent with the predictions of the DG model. Pigeons responded to occasional short-impulse IFIs that were intercalated in a series of longer IFIs by shortening their wait time in the next interval. This one-back pattern of responding is consistent with the results from prior studies on rapid timing (e.g., Higa et al., 1991; Wynne & Staddon, 1988, 1992). The experiments also showed that the local effect of an impulse (a decreased wait time in the next interval) can combine with other impulses to shorten wait

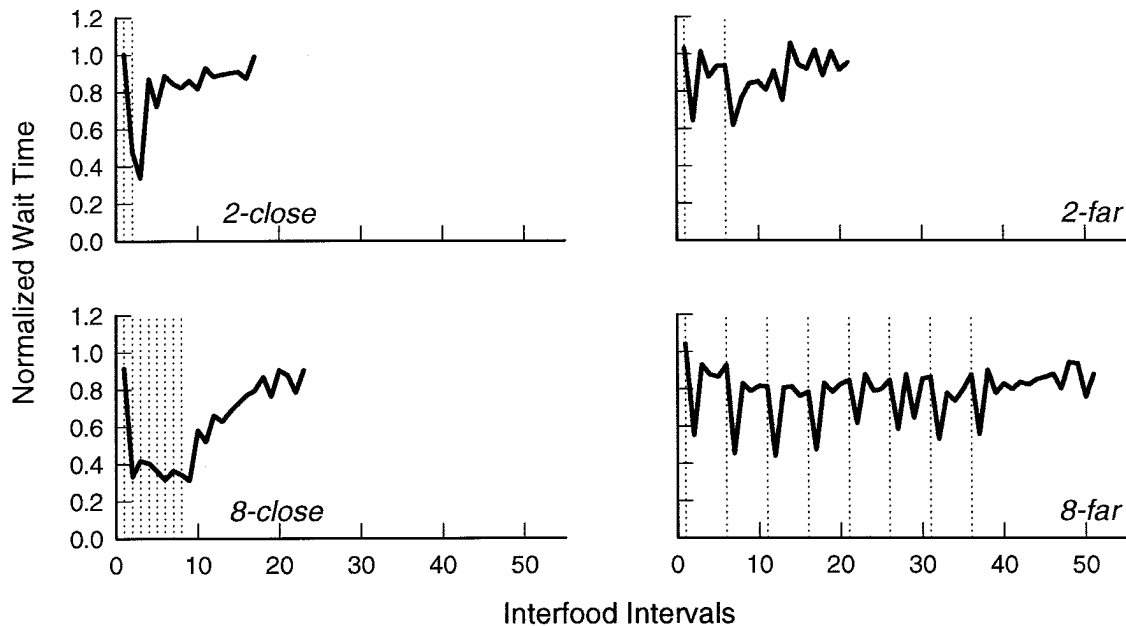


Fig. 11. Results for pigeons from Experiment 2. Only wait times (normalized, see text for details) from the set of impulses and the next 15 IFIs are shown. Data are extracted from Figure 9 for comparison with the simulation results shown in Figure 8.

times in several subsequent postimpulse intervals. For example, wait times were more suppressed below preimpulse levels (i.e., were shorter than normal) after a sequence of eight consecutive impulses than after just two. Moreover, the nonlocal effect of eight consecutive impulses was attenuated when each was separated by four longer IFIs. The basic pattern of results occurred early in training, did not appear to change systematically across sessions, and did not appear to depend on the absolute duration of the impulse and background IFIs.

These results have important implications for theories of time discrimination. Some models (e.g., SET and BeT) are based on molar features of the experimental condition. Hence, they make no predictions regarding the rapid timing effects reported here. Linear waiting (e.g., Wynne & Staddon, 1988) can account for the one-back effects of impulses but cannot explain other aspects of the data, namely, the slow recovery of wait times to longer durations after a set of eight-close impulses: Linear waiting predicts rapid recovery of wait times following all sets of impulses.

Moreover, linear waiting (and the SET and BeT models) cannot explain the range of dy-

namic data reported here and in other studies. In particular, these models cannot explain intermediate forms of linear waiting. For instance, pigeons initially track a changing temporal sequence (e.g., a 15-, 5-, 15-, 45-s cycle) according to a one-back process, but tracking degrades with further training: Wait times converge to a duration appropriate to the shortest IFI with no evidence of temporal discrimination (e.g., Higa et al., 1993).

The DG model is an alternative to other timing models. It suggests that the range of effects can be understood as interactions between individual IFIs. How much interaction occurs will depend on the frequency and recency of previous intervals. The DG model states that reinforcement at a particular post-food time increases the activation strength of the unit that represents this time. Furthermore, activation strength of that unit generalizes and diffuses to other neighboring units according to Equation 1 above. These simple, basic assumptions underlie a model that can account for the current data. For example, several successive short IFI durations will increase the activation strength of a given unit and increase the spread of effect to surrounding units—to units representing earlier and

later postfood times. The spread to, and activation of, earlier units correspond to what happens after eight consecutive impulses: A delay in the recovery of wait times to longer preimpulse durations.

The DG model can also account for dynamic data for which other theories of timing do not offer an account. For example, consider the finding that pigeons initially track a repeating series of 15-, 5-, 15-, 45-s IFIs according to a one-back process, but do not continue to do so as training progresses (Higa et al., 1993). The DG model's explanation of these data rests in its implication about the asymmetry between short and longer IFIs—that the effect of a longer IFI may be overwhelmed by the effects of shorter IFIs. Consider the following example. Suppose an animal is given several 15-s IFIs. Its tendency to respond will be a fraction of that IFI, say 5 s. If the next IFI is 45 s, the animal will probably base its wait time on the preceding IFI duration and wait 5 s. But what will the animal do if presented with another 45-s IFI? It will probably respond short at 5 s. Why? Although it has a tendency to respond long (based on the preceding 45-s IFI), it still has a strong, though weakening, tendency to respond short (based on all the other 15-s IFIs it has recently experienced). Thus, an animal fails to respond long, not necessarily because it fails to learn about the 45-s IFI but because its weakened tendency to respond short is nevertheless strong enough to preempt responding at longer wait times. Eventually, the tendency to respond short will dissipate altogether, and we may eventually see longer wait times.

Therefore, during a repeating cycle of 15-, 5-, 15-, 45-s intervals, finding short wait times in all IFIs does not mean that the animal fails to learn about the 45-s interval, but it suggests that the lower tendency to respond short preempts responding at longer wait times. In a sense, then, discrimination may be affected by a kind of proactive interference from recent experience with short IFIs. The DG model is a suggestion about how that process may arise. It can potentially account not only for rapid timing according to linear waiting but also apparent evidence against linear waiting. Furthermore, it suggests that prior studies that have reported no evidence of one-back discrimination (e.g., Innis, 1981, in

some experiments; Staddon, 1967) might, in fact, have had evidence for such a process during initial training sessions.

The present study was aimed at testing predictions of the DG model regarding the effects of the number and spacing of prior (short) IFIs on wait-time responses. Data from pigeons were compared with data from simulations of the experimental conditions. The observed results were consistent, overall, with simulations of the model. However, several issues remain unanswered. First, the DG model raises a question about the role of relatively longer IFIs. For reasons similar to those given above, it predicts that intercalating a single long IFI into a series of short IFIs will not be detected; that is, wait time following a long IFI will not necessarily increase because of preemption from shorter wait times. Experiments addressing this issue have not yet been conducted, but it would be an interesting test of the model.

Next, the results from the present experiment differed from those of the simulations in a few ways. One difference was that the model predicts successively shorter wait times after each impulse, yet this pattern was not found in either Experiment 1 or 2. Another difference was that, although the model predicts the overall pattern of wait times from both experiments, it predicts wait times that are longer than those that were observed in Experiment 2. How might these differences be accommodated? One possibility is to assume a variable threshold or different diffusion parameters for different IFI durations. In other words, the model should specify when diffusion should cease or slow down, or when a threshold for responding should remain the same or decrease (e.g., the stability-plasticity dilemma; Carpenter & Grossberg, 1987). Experimental evidence from other studies (e.g., Higa et al., 1993; Wynne & Staddon, 1992) suggests that short IFIs (e.g., shorter than 20 or 30 s) have a stronger effect on wait-time responses than do longer IFIs (longer than 30 s). Therefore, assuming variable threshold and diffusion parameters is not unreasonable. Further research should determine whether such modifications will improve the model.

In summary, the results from the present study confirm that time discrimination can be understood from interactions among IFIs;

however, the process is more complex than simple linear waiting (e.g., Wynne & Staddon, 1988): Wait-time responses may be based on the frequency and recency of prior IFIs. The DG model suggests how IFIs interact to influence time discrimination. Although it does not capture all of the effects associated with time discrimination, the model draws attention to some of its fundamental dynamic properties and provides a starting point for understanding the underlying processes.

REFERENCES

- Carpenter, G. A., & Grossberg, S. (1987). A massively parallel architecture for a self-organizing neural pattern recognition machine. *Computer Vision, Graphics, and Image Processing*, *37*, 54–115.
- Church, R. M., & Broadbent, H. A. (1991). A connectionist model of timing. In M. L. Commons, S. Grossberg, & J. E. R. Staddon (Eds.), *Neural network models of conditioning and action* (pp. 225–240). Hillsdale, NJ: Erlbaum.
- Dews, P. (1970). The theory of fixed-interval responding. In W. N. Schoenfeld (Ed.), *The theory of reinforcement schedules* (pp. 43–61). New York: Appleton-Century-Crofts.
- Ferster, C. B., & Skinner, B. F. (1957). *Schedules of reinforcement*. New York: Appleton-Century-Crofts.
- Fetterman, J. G., & Killeen, P. R. (1991). Adjusting the pacemaker. *Learning and Motivation*, *22*, 226–252.
- Gibbon, J. (1977). Scalar expectancy and Weber's law in animal timing. *Psychological Review*, *84*, 279–325.
- Gibbon, J. (1995). Dynamics of time matching: Arousal makes better seem worse. *Psychonomic Bulletin & Review*, *2*, 208–215.
- Gibbon, J., & Allan, L. (Eds.). (1984). Timing and time perception. *Annals of the New York Academy of Sciences: Vol. 423*. New York: New York Academy of Sciences.
- Gibbon, J., & Balsam, P. (1981). Spreading association in time. In C. M. Locurto, H. S. Terrace, & J. Gibbon (Eds.), *Autoshaping and conditioning theory* (pp. 219–251). San Diego: Academic Press.
- Gibbon, J., & Church, R. M. (1984). Sources of variance in an information processing theory of timing. In H. L. Roitblat, T. G. Bever, & H. S. Terrace (Eds.), *Animal cognition* (pp. 465–488). Hillsdale, NJ: Erlbaum.
- Gibbon, J., Church, R. M., & Meck, W. H. (1984). Scalar timing in memory. In J. Gibbon & L. Allan (Eds.), *Timing and time perception* (pp. 52–77). New York: New York Academy of Sciences.
- Higa, J. J., Thaw, J. M., & Staddon, J. E. R. (1993). Pigeons' wait-time responses to transitions in interfood interval duration: Another look at cyclic schedule performance. *Journal of the Experimental Analysis of Behavior*, *59*, 529–541.
- Higa, J. J., Wynne, C. D. L., & Staddon, J. E. R. (1991). Dynamics of time discrimination. *Journal of Experimental Psychology: Animal Behavior Processes*, *17*, 281–291.
- Innis, N. K. (1981). Reinforcement as input: Temporal tracking on cyclic interval schedules. In M. L. Commons & J. A. Nevin (Eds.), *Quantitative analysis of behavior: Discriminative properties of reinforcement schedules* (pp. 257–286). New York: Pergamon Press.
- Innis, N. K., Cooper, S. J., & Mitchell, S. K. (1993). The determinants of postreinforcement pausing. *Behavioural Processes*, *29*, 229–238.
- Killeen, P. R., & Fetterman, J. G. (1988). A behavioral theory of timing. *Psychological Review*, *95*, 274–295.
- Meck, W. H., Komeily-Zadeh, F. N., & Church, R. M. (1984). Two-step acquisition: Modification of an internal clock's criterion. *Journal of Experimental Psychology: Animal Behavior Processes*, *10*, 297–306.
- Mellon, R. C., Leak, T. M., Fairhurst, S., & Gibbon, J. (1995). Timing processes in the reinforcement omission effect. *Animal Learning & Behavior*, *23*, 286–296.
- Richelle, M., & Lejeune, H. (1980). *Time in animal behavior*. Oxford: Pergamon Press.
- Schneider, B. A. (1969). A two-state analysis of fixed-interval responding in the pigeon. *Journal of the Experimental Analysis of Behavior*, *12*, 677–687.
- Shull, R. L. (1970a). A response-initiated fixed-interval schedule of reinforcement. *Journal of the Experimental Analysis of Behavior*, *13*, 13–15.
- Shull, R. L. (1970b). The response-reinforcement dependency in fixed-interval schedules of reinforcement. *Journal of the Experimental Analysis of Behavior*, *14*, 55–60.
- Skinner, B. F. (1938). *The behavior of organisms*. New York: Appleton-Century-Crofts.
- Staddon, J. E. R. (1967). Attention and temporal discrimination: Factors controlling responding under a cyclic-interval schedules. *Journal of the Experimental Analysis of Behavior*, *10*, 349–359.
- Staddon, J. E. R. (1974). Temporal control, attention and memory. *Psychological Review*, *81*, 375–391.
- Staddon, J. E. R., & Higa, J. J. (1991). Temporal learning. In G. H. Bower (Ed.), *The psychology of learning and motivation* (Vol. 27, pp. 265–294). San Diego: Academic Press.
- Staddon, J. E. R., & Reid, A. K. (1990). On the dynamics of generalization. *Psychological Review*, *97*, 576–578.
- Wynne, C. D. L., & Staddon, J. E. R. (1988). Typical delay determines waiting time on periodic-food schedules: Static and dynamic tests. *Journal of the Experimental Analysis of Behavior*, *50*, 197–210.
- Wynne, C. D. L., & Staddon, J. E. R. (1992). Waiting in pigeons: The effects of daily intercalation on temporal discrimination. *Journal of the Experimental Analysis of Behavior*, *58*, 47–66.

Received January 16, 1996
Final acceptance March 25, 1996